

From surface to caves: new species of *Diploexochus* Brandt, 1833 (Oniscidea, Armadillidae) from Colombia, with the description of the first troglobitic species

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Abstract

Two new species of *Diploexochus* are described, *Diploexochus cacique* sp. nov. from Cerro Bañaderos in Hatonuevo, La Guajira, and *Diploexochus troglobius* sp. nov. from Roca Madre Cave, Toluviejo, Sucre, both from the Tropical Dry Forest (TDF) areas of the Colombian Caribbean. The latter represent the first troglobitic species of the genus. Moreover, based on specimens from Sierra Nevada de Santa Marta, Magdalena (type locality), *Venezillo brevispinis* is placed into *Diploexochus* and an identification key for all species of the genus is given. The present work describes the first troglobitic species of the genus, and expand the knowledge of its distribution in northern South America.

Key words: Cave-dwelling, Colombian Caribbean, Neotropical, subterranean systems, terrestrial isopods, Tropical Dry Forest

Introduction

Terrestrial isopods (Oniscidea) are considered one of the most diverse groups of crustaceans, comprising approximately 4,000 species in more than 500 genera in 38 or 39 families, distributed in almost all terrestrial habitats, including caves (Schmalfuss 2003; Hornung 2011; Sfenthourakis and Taiti 2015; Campos-Filho et al. 2017a, 2018, 2023a, 2023b; Taiti 2017; Dimitriou et al. 2019; Campos-Filho and Taiti 2021). Within Oniscidea, the family Armadillidae Brandt, 1831 is the most diverse, including more than 600 species in 81 genera and distributed in Neotropical, Afrotropical, Oriental, and Australian regions (Taiti et al. 1998; Schmalfuss 2003; Sfenthourakis and Taiti 2015; Rodríguez-Cabrera and Armas 2023). In Colombia, 13 species of the family are known: *Ctenorillo binomio* Carpio-Díaz, Bichuette & Campos-Filho, 2023, *C. dazai* Carpio-Díaz, López-Orozco & Campos-Filho, 2018, *C. humboldti* Carpio-Díaz, López-Orozco & Campos-Filho,

2023, *C. mincaensis* López-Orozco, Carpio-Díaz & Campos-Filho, 2023, *C. orientalis* Carpio-Díaz, Taiti & López-Orozco, 2023, *C. papagayoensis* Carpio-Díaz, Borja-Arrieta & Campos-Filho, 2023, *C. tayrona* López-Orozco, Borja-Arrieta & Campos-Filho, 2023, *C. tuberosus* (Budde-Lund, 1904), *Synarmadillo ruthveni* (Pearse, 1915), *Venezillo brevispinis* (Pearse, 1915), *V. gigas* (Miers, 1877), *V. grenadensis* (Budde-Lund, 1893), and *V. vincentis* (Budde-Lund, 1904) (Richardson 1912; Pearse 1915; Carpio-Díaz et al. 2018, 2023a; López-Orozco et al. 2022).

The genus *Diploexochus* Brandt, 1833 comprises five species exclusively distributed in South America, i.e., *D. echinatus* Brandt, 1833 from Brazil, French Guiana, Guyana, and Trinidad, *D. obscurus* Cardoso, Bastos-Pereira & Ferreira, 2022, *D. spinatus* Cardoso, Bastos-Pereira & Ferreira, 2022, *D. carrapicho* Campos-Filho, López-Orozco & Taiti, 2023, and *D. exu* Campos-Filho, Sfenthourakis & Bichuette, 2023 from Brazil (Schmalfuss 2003; Campos-Filho et al. 2023a; Cardoso et al. 2023). The genus is characterized by the shape and direction of the pereonites 1–7 epimera and pleonites 3–5 epimera, large schisma of the pereonite 1 epimera, frontal shield surpassing the vertex of the cephalon, and the presence of well-developed dorsal tubercles (see Campos-Filho et al. 2017a).

According to the Sector Technical Standard NTS-AV012 of 2008, a cavern is defined as any subterranean space within rocks large enough for human entry; it may have been formed in rocks or ice and may be filled with water, sediments, blocks, lava, and sometimes it may be impenetrable. The environmental conditions in these habitats are stable and support the establishment of various forms of life, including troglobitic organisms. These organisms are characterized by completing their entire life cycle within caves and exhibit high degree of troglomorphism (Galán and Herrera 1998). Various subterranean systems have been reported in Colombia, especially for the department of Santander, where most of the studies are concentrated (Muñoz-Saba et al. 1998a, 1998b; 2013; Castellanos-Morales et al. 2015; Barriga et al. 2019; Valdivieso 2022). Despite this, the associated diversity for most caves is still only estimated, particularly in the Caribbean region, where the number of subterranean systems remains unknown.

The diversity of Oniscidea from Colombia has increased considerably in the last years (López-Orozco et al. 2014, 2016, 2017, 2022; Carpio-Díaz et al. 2016, 2018, 2021, 2023a, 2023b; Campos-Filho et al. 2020). However, this knowledge is far from complete, considering the territorial extension of the country which difficult extensive surveys. In this study, two new species of *Diploexochus* are described for the department of La Guajira and Sucre. Moreover, the examination of specimens of *V. brevispinis* from Sierra Nevada de Santa Marta, Magdalena Department (type locality), allowed the placement of the species into the genus *Diploexochus*. Additionally, an identification key for the species and ecological and conservation remarks are provided.

Materials and methods

The specimens were preserved in 70% ethanol. Identifications were based on morphological characters using micropreparations in Hoyer's medium (Anderson 1954). Illustrations were made with aid of a camera lucida mounted on Wild M3 and M20 microscopes. The images of the species were obtained using a stereomicroscope SteREO Discovery.V12 ZEISS with an adapted camera

Axiocam ERc 5s. The final illustrations were created using GIMP software (v. 2.8) following the method proposed by Montesanto (2015, 2016). Respiratory structures were classified according to Paoli et al. (2002). The examined material is deposited in the Collection of the University of Cartagena, Cartagena, Colombia (CBUDC-CRU).

Results

Systematics

Suborder Oniscidea Latreille, 1802

Family Armadillidae Brandt, 1831

Genus *Diploexochus* Brandt, 1833

Type species. *Diploexochus echinatus* Brandt, 1833, by monotypy (see Schmidt and Leistikow 2004).

Diploexochus brevispinis (Pearse, 1915), comb. nov.

Figs 1–4, 8A, 13A

Cubaris brevispinis Pearse, 1915: 543, fig. 5.

Cubaris brevispinis: Van Name 1936: 382, fig. 232.

Venezillo (Vandelillo) brevispinis: Arcangeli 1957: 121.

Venezillo brevispinis: Leistikow and Wägele 1999: 47; Schmalfuss 2003: 286.

Material examined. COLOMBIA • 1♂, 1♀ (parts in micropreparations), Hacienda Cafetera Cincinnati, Sierra Nevada de Santa Marta, Santa Marta, Magdalena, 11°6'34.14"N, 74°5'30.84"W, leg. CM López-Orozco, YM Carpio-Díaz, 13.VIII. 2018, CBUDC-CRU 344 • 3♂, 4♀, same locality and collectors as for preceding, CBUDC-CRU 343.

Redescription. Maximum body length: male 7 mm, female 7.5 mm. Color dark brown, cephalon, pereon, pleon, and telson strongly pigmented, pleonites 3–5 epimera less pigmented (Fig. 8A); upper portion of tubercles, pereonite 1 epimera anterior and posterior corners, pereonites 2, 3, and 6 epimera weakly pigmented, sometimes depigmented. Color pattern preserved in ethanol (Figs 2A, 13A). Body in lateral view as in Fig. 2A. Endoantennal conglobation (Figs 2A, 13A). Dorsum covered with large triangular tubercles, arranged as follows (Fig. 2A, B): vertex of cephalon with 10 tubercles in three rows; pereonite 1 with 25–29 tubercles; pereonites 2–6 with 17 tubercles; pereonite 7 with 15 tubercles; pleonites 3–5 with one tubercle on median portion, and telson with two paramedian tubercles. Pereonites 1–7 epimera with one line of *noduli laterales* per side inserted on outer surface of second tubercle of posterior row (Fig. 2A). Dorsal surface with short semi-circular scale-setae (Fig. 2C). Cephalon (Fig. 2D–F) with frontal shield prominent, distinctly protruding above vertex; eyes of 16 ommatidia. Pereonites 1–7 epimera flattened and directed outwards; pereonite 1 strongly grooved on lateral margin, inner lobe of schisma rounded, not extending beyond posterior margin of outer lobe (Fig. 2G–H), pereonite 2 with triangular ventral lobe obliquely directed backwards; pereonites 3–7 with

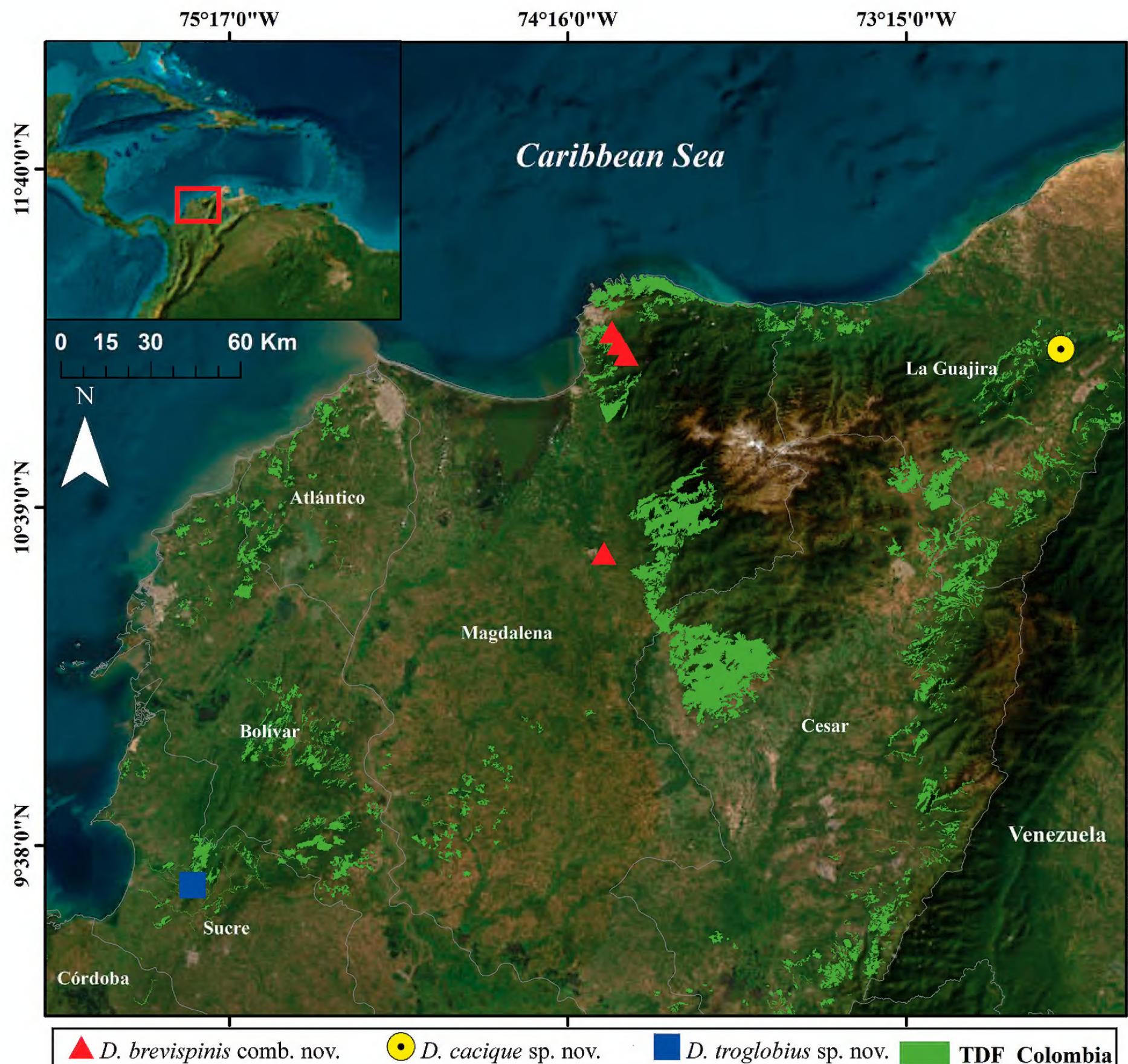


Figure 1. Distribution map of the *Diploexochus* species from Colombia. Green areas: Tropical Dry Forest (TDF) from Colombia (García et al. 2014).

oblique ventral ridge (Fig. 2A–G). Pleonites 3–5 (Fig. 2I, J) with epimera well developed, rectangular, and directed outwards. Telson (Fig. 2I) with proximal part slightly broader than distal part, dorsum slightly depressed, distal margin straight. Antennula (Fig. 2K) of three articles, proximal article longest, distal article with five aesthetascs inserted apically. Antenna (Fig. 2L) short, not surpassing posterior margin of pereonite 1 when extended backwards; flagellum of two articles, distal article about three times as long as first bearing one row of two lateral aesthetascs. Mandibles with molar penicil dichotomized; left mandible (Fig. 3A) with 2+1 penicils, right mandible (Fig. 3B) with 1+1 penicils. Maxillula (Fig. 3C) inner endite with two stout penicils; outer endite with 4+6 simple teeth. Maxilla (Fig. 3D) inner lobe rounded and covered with thick setae; outer lobe rounded, twice as wide as inner lobe, covered with thin setae. Maxilliped (Fig. 3E) basis rectangular bearing sparse setae; palp with two distinct setae on basal article; endite subrectangular, medial seta overpassing distal margin, distal mar-

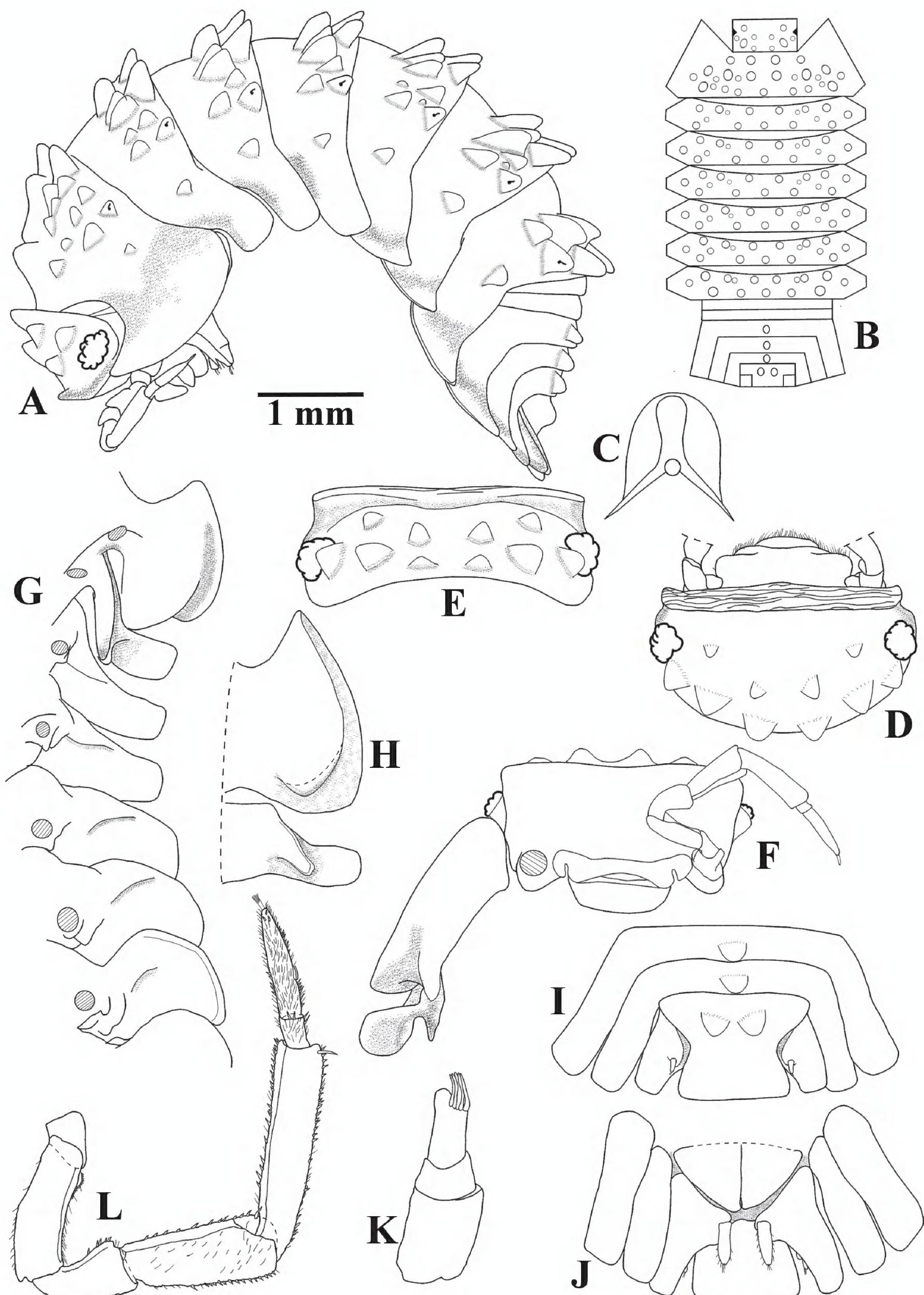


Figure 2. *Diploexochus brevispinis* (Pearse, 1915), comb. nov. (♀ CBUDC-CRU 344) **A** habitus, lateral view **B** dorsal tubercles scheme **C** dorsal scale-seta **D** cephalon, dorsal view **E** cephalon, posterior view **F** cephalon and pereonites 1 and 2, frontal view **G** pereonites 1–7 epimera, ventral view **H** pereonites 1 and 2 epimera, ventral view **I** pleonites 4 and 5, telson, and uropods, dorsal view **J** pleonites 4 and 5, telson, and uropods, ventral view **K** antennula **L** antenna.

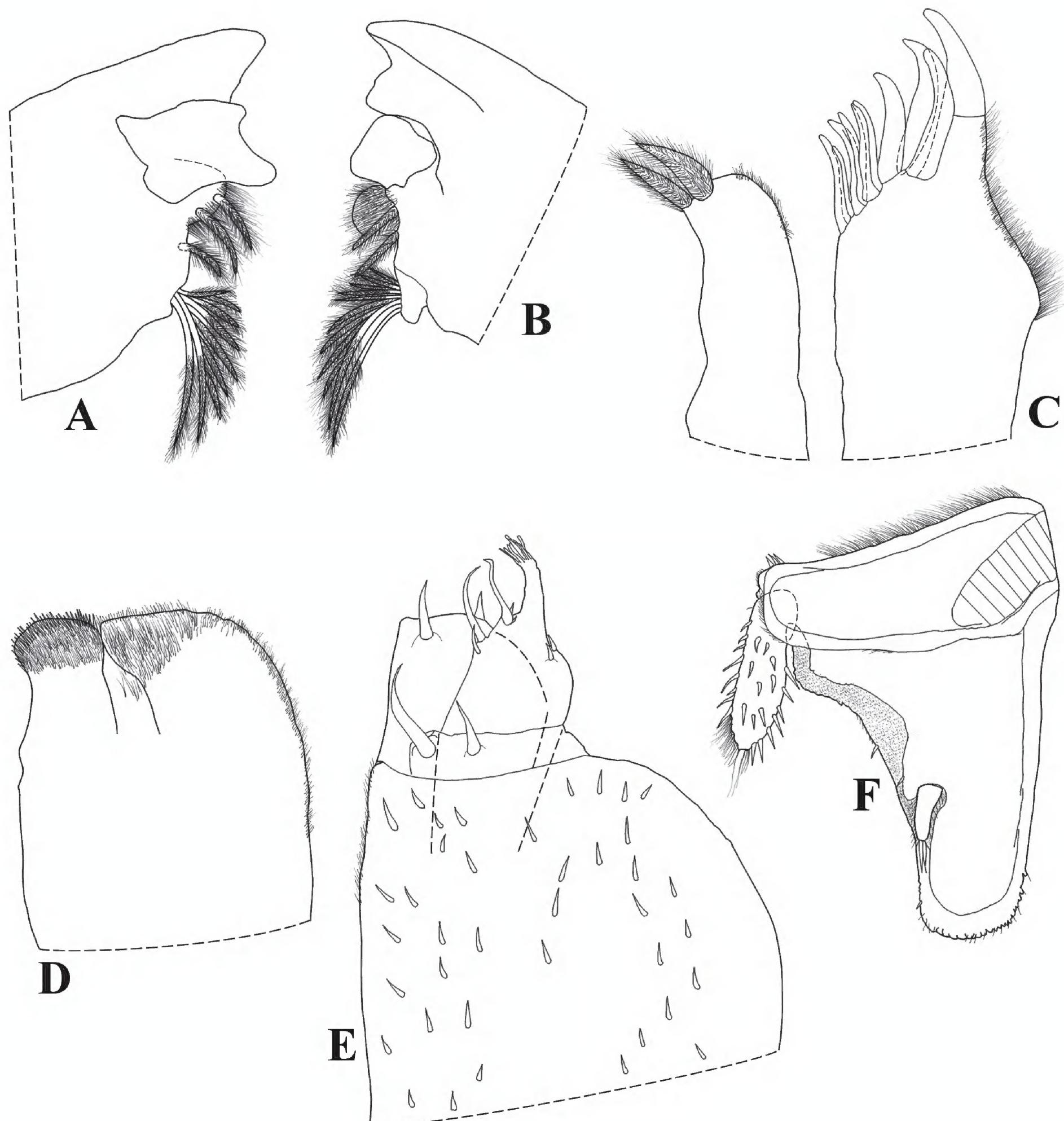


Figure 3. *Diploexochus brevispinis* (Pearse, 1915), comb. nov. (♀ CBUDC-CRU 344) **A** left mandible **B** right mandible **C** maxillula **D** maxilla **E** maxilliped **F** uropod.

gin with one short seta. Pereopods 1–7 merus and carpus with sparse setae on sternal margin; carpus 1 with distal setae cleft at apex; ungual seta and dactylar organ simple. Uropod (Fig. 3F) protopod flattened, enlarged on basal part, distal part subrectangular, medial margin slightly concave; exopod short, inserted dorsally near medial margin below distinct lobe, lobe not extending beyond medial margin. Pleopod exopods 1–5 with monospiracular respiratory structures.

Male. Pereopods 1–7 (Fig. 4A, B) without particular modifications. Genital papilla as in Fig. 5C. Pleopod 1 (Fig. 4D) exopod triangular, wider than long, outer and inner margin bearing many small setae, distal part triangular, proximal

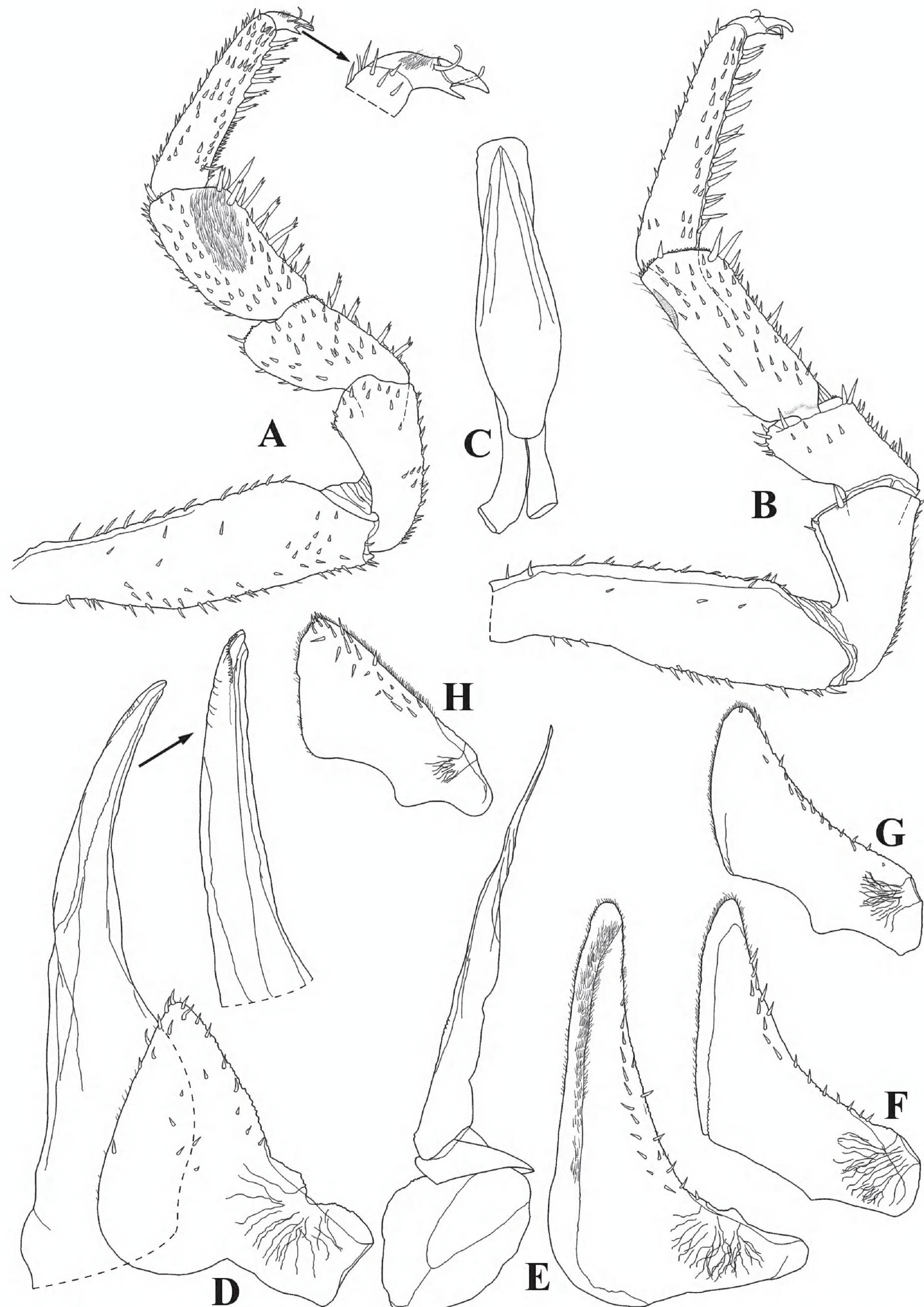


Figure 4. *Diploexochus brevispinis* (Pearse, 1915), comb. nov. male (♂ CBUDC-CRU 344) **A** pereopod 1 **B** pereopod 7 **C** genital papilla **D** pleopod 1 **E** pleopod 2 **F** pleopod 3 exopod **G** pleopod 4 exopod **H** pleopod 5 exopod.

outer part quadrangular; endopod about twice as long as exopod, distal portion slightly directed outwards. Pleopod 2 (Fig. 4E) exopod triangular, outer margin strongly concave bearing many setae; endopod longer than exopod. Pleopod 3–5 exopods as in Fig. 4F–H.

Remarks. Pearse (1915) described *Cubaris brevispinis* from Minca, Sierra Nevada de Santa Marta, Colombia. Vandel (1952) proposed new morphological characters for the genus *Venezillo*, such as the shape of the epimera and ventral lobes of pereonites 1 and 2. Arcangeli (1957), based on the previous characters, transferred *C. brevispinis* to the genus *Venezillo*, at that time within the subgenus *Vandelillo*.

Among the characteristics mentioned by Pearse (1915), the number and arrangement of the dorsal tubercles of the cephalon, pereonites 2–7, pleon, and telson, the shape and direction of the pereonites 1–7 epimera, and the number of ommatidia were confirmed here. The only distinct characteristic contrasting with the original description was the number of tubercles on pereonite 1. Pearse reported 29 tubercles, while 25 were observed in the present study. Probably, this difference is related with the size of the specimens. Additionally, in the drawings of Pearse, the lateral schisma of the pereonite 1 epimera reached about half of its length, which was also confirmed here [see Fig. 2F–H for comparison with Pearse (1915)]. Thus, based on the generic diagnostic characters mentioned previously, *V. brevispinis* is placed into the genus *Diploexochus*.

Diploexochus brevispinis comb. nov. easily differs from *D. carrapicho*, *D. echinatus*, *D. exu*, *D. obscurus*, and *D. spinatus* in the number and arrangement of the dorsal tubercles of the cephalon, pereon, and pleon. Moreover, it differs in having the antennula with five distal aesthetascs (vs six in *D. exu* and *D. carrapicho*, 10 in *D. echinatus*, seven in *D. obscurus*, and nine in *D. spinatus*), mandibles with dichotomized molar penicil (vs simple in all species), and uropod protopod with median lobe not protruding beyond the medial margin (vs protruding in all species) (see Campos-Filho et al. 2017a, 2023a; Cardoso et al. 2023).

Natural history. Specimens of *Diploexochus brevispinis* comb. nov. were collected under fallen logs in a sub-Andean forest close to the road at the Cincinnati farm in the Sierra Nevada de Santa Marta, Magdalena, Colombia (Fig. 8A).

Distribution. This species is known only from its type locality in Tropical Dry Forest (TDF) and Andean forest of Sierra Nevada de Santa Marta (Fig. 1).

Diploexochus cacique López-Orozco, Carpio-Díaz & Campos-Filho, sp. nov.

<https://zoobank.org/3BD3757B-7DFF-4554-B456-09AFC7AF3E2E>

Figs 1, 5–7, 8B, 13B

Type material. COLOMBIA • 1♂, **holotype**, Cerro Bañaderos, Hatonuevo, La Guajira, 11°7'33.3"N, 72°47'6.9"W, 12.I.2016, leg. M Gutierrez-Estrada, CBUC-CRU 350 • 1♂, 1♀ (parts in micropreparations), **paratypes**, same data as holotype, CBUDC-CRU 413 • 1♀, **paratypes**, same data as holotype, CBUDC-CRU 414.

Description. Maximum body length: male 8 mm, female 9 mm. Body outline as in Fig. 5A. Color dark brown with typical muscular insertions (Figs 8B, 13B); upper portion of tubercles randomly depigmented; pereonite 1 epimera anterior corner, pereonites 2–7 paramedian portions, pereonites 3 and 4

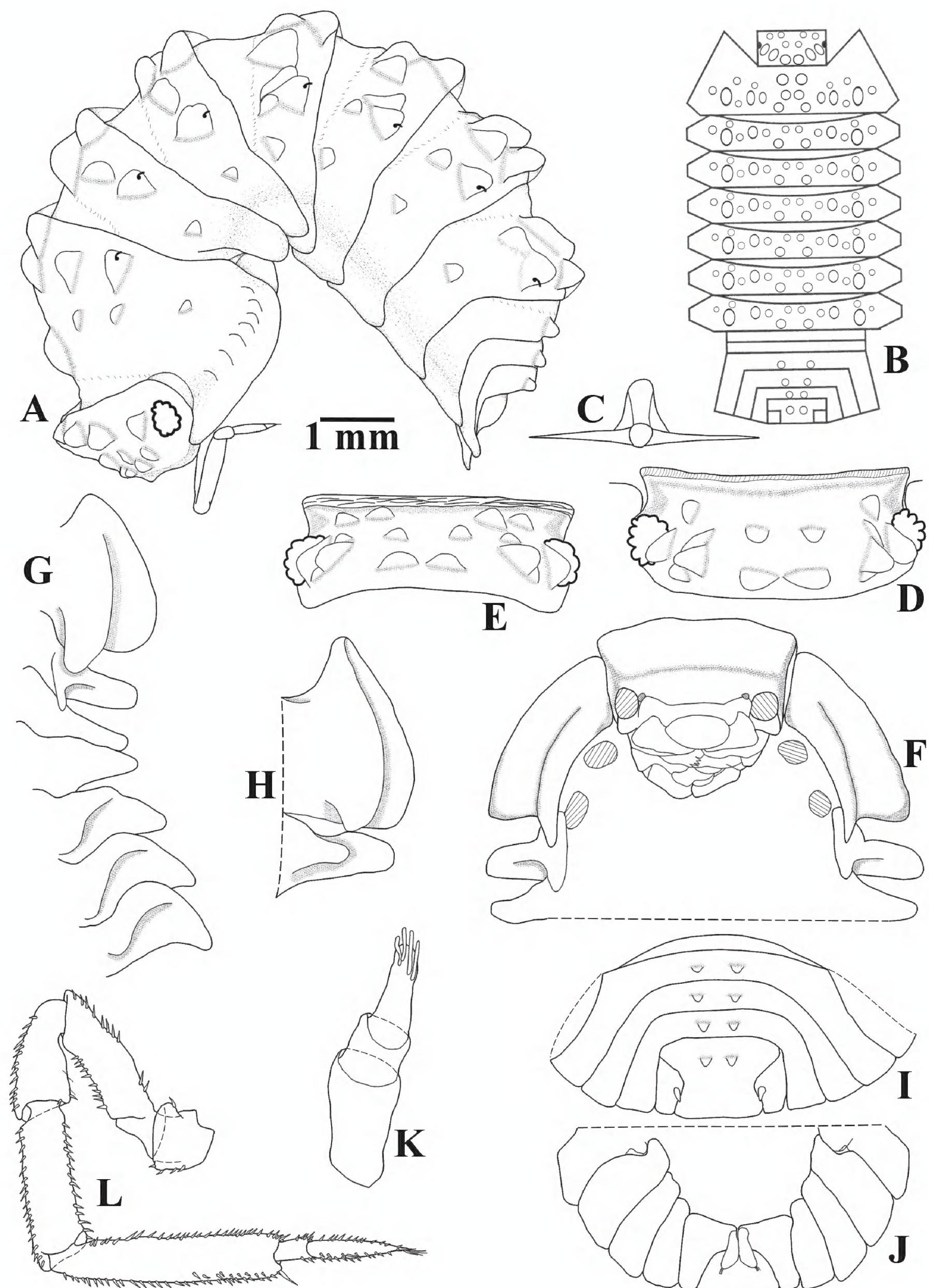


Figure 5. *Diploexochus cacique* López-Orozco, Carpio-Díaz & Campos-Filho, sp. nov. (♀ paratype, CBUDC-CRU 413) **A** habitus, lateral view **B** dorsal tubercles scheme **C** dorsal scale-seta **D** cephalon, dorsal view **E** cephalon, posterior view **F** cephalon and pereonites 1–3, frontal view **G** pereonites 1–7 epimera, ventral view **H** pereonites 1 and 2 epimera, ventral view **I** pereonites 3–5, telson, and uropods, dorsal view **J** pleonites 3–5, telson, and uropods, ventral view **K** antennula **L** antenna.

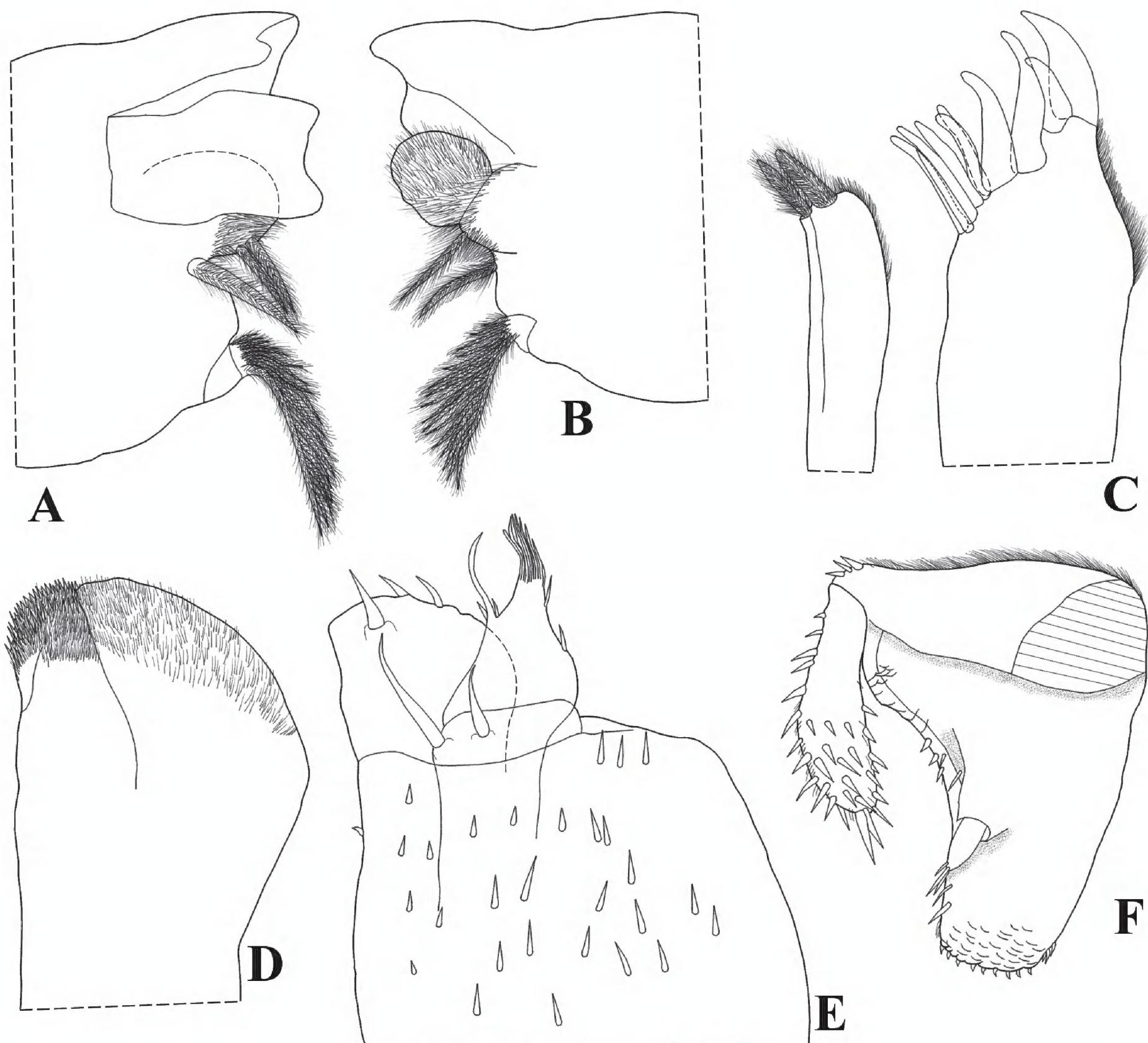


Figure 6. *Diploexochus cacique* López-Orozco, Carpio-Díaz & Campos-Filho, sp. nov. (♀ paratype, CBUDC-CRU 413) **A** right mandible **B** left mandible **C** maxillula **D** maxilla **E** maxilliped **F** uropod.

epimera, and pleonites 3–5 epimera randomly depigmented. Endoantennal conglobation (Figs 5A, 8B, 13B). Dorsum covered with large triangular tubercles, arranged as follows (Fig. 5A, B): vertex of cephalon with 12 tubercles in three rows; pereonite 1 with 20 tubercles; pereonites 2–6 with 16 tubercles; pereonite 7 with 15 tubercles; pleonites 3–5 and telson with two paramedian tubercles. Pereonites 1–7 epimera with one line of ***noduli laterales*** per side inserted on outer surface of second tubercle of posterior row (Fig. 5A). Dorsal surface with short and narrow semi-circular scale-setae (Fig. 5C). Cephalon (Fig. 5D–F) with frontal shield prominent, distinctly protruding above vertex; eyes with 20–21 ommatidia. Pereonites 1–7 epimera flattened and slightly directed outwards; pereonite 1 strongly grooved on lateral margin, inner lobe of schisma rounded, extending beyond posterior margin of outer lobe (Fig. 5G, H), pereonite 2 with triangular and narrow ventral lobe directed outwards, not extending beyond posterior margin of epimera; pereonites 4–7 with oblique ventral ridge (Fig. 5F–H). Pleonites 3–5 (Fig. 5I, J) with epimera well devel-

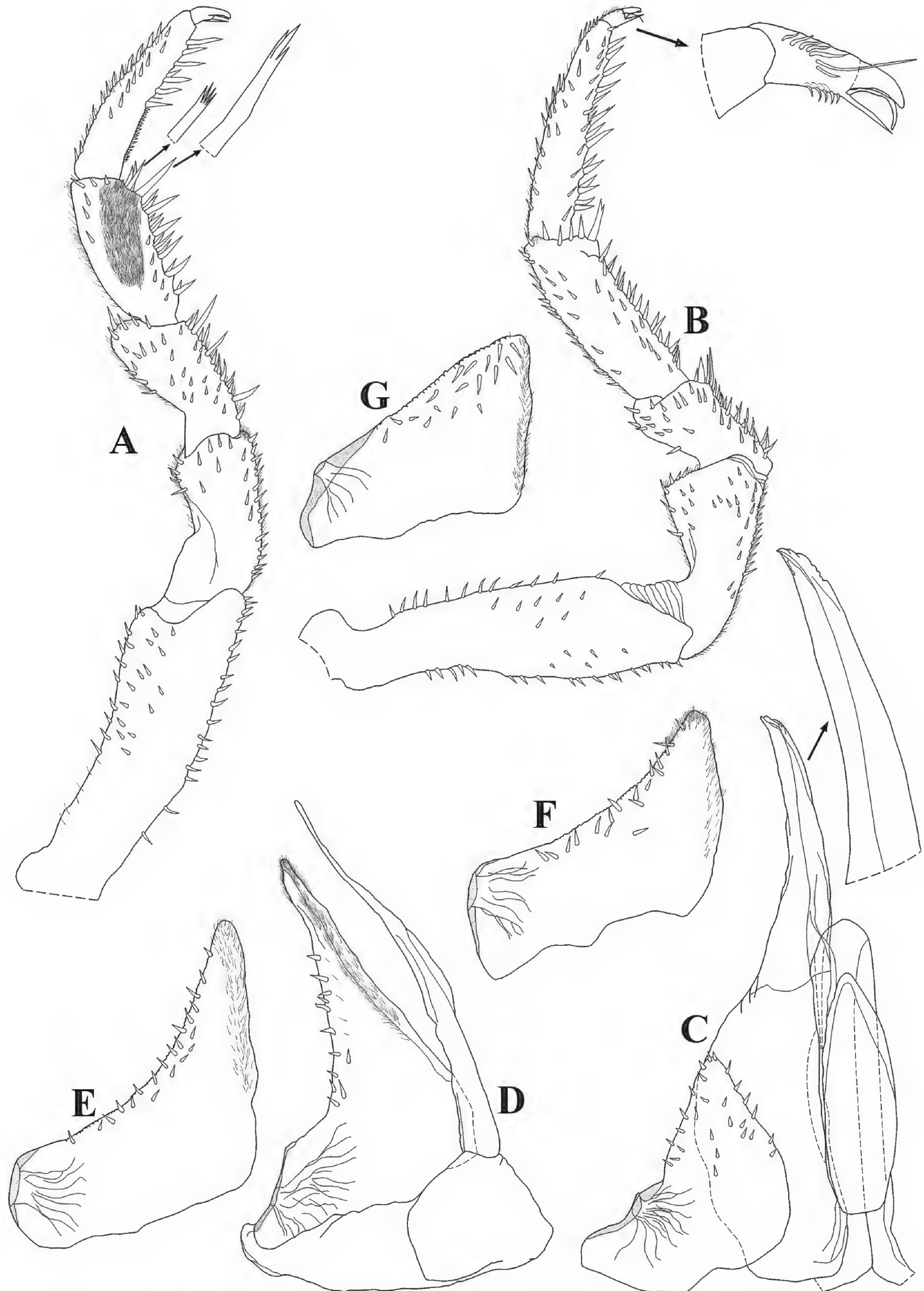


Figure 7. *Diploexochus cacique* López-Orozco, Carpio-Díaz & Campos-Filho, sp. nov. (♂ paratype, CBUDC-CRU 413) **A** pereopod 1 **B** pereopod 7 **C** pleopod 1 and genital papilla **D** pleopod 2 **E** pleopod 3 exopod **F** pleopod 4 exopod **G** pleopod 5 exopod.



Figure 8. **A** *Diploexochus brevispinis* (Pearse, 1915), comb. nov. under fallen tree in the Sierra Nevada de Santa Marta, Magdalena **B** *Diploexochus cacique* López-Orozco, Carpio-Díaz & Campos-Filho, sp. nov. on the tree bark, Cerro Bañaderos, Hato Nuevo, La Guajira.

oped, rectangular and slightly directed outwards. Telson (Fig. 5I) with proximal part slightly broader than distal part, dorsum slightly depressed, distal margin straight. Antennula (Fig. 5K) of three articles, proximal and distal articles subequal in length, distal article with four aesthetascs inserted sub-apically. Antenna (Fig. 5L) short, not surpassing posterior margin of pereonite 1 when extended backwards; flagellum of two articles, distal article about twice as long as first bearing one row of two lateral aesthetascs. Mandibles with molar penicil semi-dichotomized; left mandible (Fig. 6A) with 2+1 penicils, right mandible (Fig. 6B) with 1+1 penicils. Maxillula (Fig. 6C) inner endite with two stout penicils, distal margin bearing fringe of thin setae; outer endite of 4+6 teeth simple. Maxilla (Fig. 6D) inner lobe rounded covered with thick setae; outer lobe rounded, three times as wide as inner lobe, covered with thin setae. Maxilliped (Fig. 6E) basis rectangular bearing sparse setae; palp with two distinct setae on basal article; endite subrectangular, medial seta overpassing distal margin, distal margin bearing two setae. Pereopods 1–7 merus and carpus bearing setae on sternal margin, not sparse appearance; carpus 1 with distal setae cleft at apex; unguial seta and dactylar organ simple, both surpassing outer claw. Uropod (Fig. 6F) protopod flattened, enlarged on basal part, distal part subrectangular, medial margin concave; exopod short inserted dorsally near medial margin below distinct lobe, lobe not extending beyond medial margin; endopod club-shaped bearing many short setae on distal part. Pleopods 1–5 exopods with monospiracular respiratory structures.

Male. Pereopods 1–7 (Fig. 7A, B) without particular modifications. Genital papilla as in Fig. 9C. Pleopod 1 (Fig. 7C) exopod triangular, as wide as long, outer and inner margin bearing many small setae, distal and proximal outer parts triangular; endopod about twice as long as exopod. Pleopod 2 (Fig. 7D) exopod triangular, outer margin strongly concave bearing many setae; endopod slightly longer than exopod. Pleopod 3–5 exopods as in Fig. 7E–G.

Etymology. The new species is named after the Vallenato music singer Diomedes Díaz Maestre, also known as “El Cacique de la Junta”.

Remarks. *Diploexochus cacique* sp. nov. easily differs from the previously mentioned species in the pattern of the dorsal tubercles of the pleon and telson, the pereonites 1 and 2 epimera with ventral lobes surpassing the posterior margin of the epimera, and the club-shaped uropod endopod.

Natural history. Specimens of *Diploexochus cacique* sp. nov. were collected on tree bark around the Luis Pablo Ojeda Cave (Bañaderos cave), Cerro Bañaderos, Hatonuevo, La Guajira (Fig. 8B). The area where the *D. cacique* sp. nov. species is found is composed of TDF and is part of the Sierra de Bañadero integrated management district (DMI), a mountain system in the upper basin of the Camarones River in the department of La Guajira, which is connected to the Sierra Nevada de Santa Marta.

Distribution. This species is known only from the type locality at Cerro Bañaderos, Hatonuevo, La Guajira, which is included into a TDF area (Fig. 1).

***Diploexochus troglobius* López-Orozco, Borja-Arrieta & Campos-Filho, sp. nov.**

<https://zoobank.org/0EB8C9FC-F2AD-4D8F-963F-412AE50B7586>

Figs 1, 9–13C

Type material. COLOMBIA • 1♂, *holotype*, Roca madre Cave, Campo Aventura Roca Madre, La Piche, Toluviejo, Sucre, 9°30'50.2"N, 75°23'36.6"W, 12.VII.2018, leg. CM López-Orozco, R Borja-Arrieta, CBUDC-CRU 393 • 1♂, *paratypes*, same data as holotype, CBUDC-CRU 394 • 1♂, 1♀ (parts in micro-preparations), *paratypes*, same data as holotype, CBUDC-CRU 396.

Description. Maximum body length: male 2.7 mm, female 4.2 mm. Body outline as in Fig. 9A. Color faintly brown; body pigments not discernible in vivo (Fig. 12D). Endoantennal conglabation (Figs 9A, 12D, 13C). Dorsum covered with large triangular tubercles, arranged as follows (Fig. 9A, B): vertex of cephalon with 10 tubercles in two rows; pereonite 1 with 19 tubercles; pereonites 2–6 with 13 tubercles; pereonite 7 with 11 tubercles; pleonites 3, 4, and telson with two median tubercles. Pereonites 1–7 epimera with one line of *noduli laterales* per side inserted on outer surface of second tubercle of posterior row (Fig. 9A). Dorsal surface densely covered with elongated semi-circular scale-setae, conferring pilous aspect (Fig. 9C). Cephalon (Fig. 9D–F) with prominent frontal shield, distinctly protruding above vertex; eyes with four ommatidia. Pereonites 1–7 epimera flattened and slightly directed outwards; pereonite 1 grooved on posterior lateral margin, inner lobe of schisma rounded and extending beyond posterior margin of outer lobe. Pereonite 2 with triangular ventral lobe rounded at apex, extending beyond posterior margin of epimera; pereonites 3 and 5–7 with well-marked ventral ridge (Fig. 9A, F, G). Pleonites 3–5 epimera (Fig. 9H, I) well developed, sub-rectangular, and directed outwards, distal margins rounded. Telson (Fig. 9H) with proximal part broader than distal part, dorsum slightly depressed, distal margin sinuous. Antennula (Fig. 9J) of three articles, proximal and distal sub-equal in length, distal article with five stout aesthetascs inserted sub-apically. Antenna (Fig. 9K) short, not surpassing posterior margin of pereonite 1 when extended backward; flagellum of two articles, the distal about three times as long as first, bearing one row of two lateral aesthetascs. Mandibles with molar penicil semi-dichotomized; left mandible (Fig. 10A) with 2+1 penicils, right mandible (Fig. 10B) with 1+1 penicils. Maxillula (Fig. 10C) inner endite with two stout penicils, distal margin bearing thin setae; outer endite with 4+6 teeth simple. Maxilla (Fig. 10D) inner lobe rounded covered with thick setae; outer lobe rounded three times as wide as inner lobe covered with thin setae.

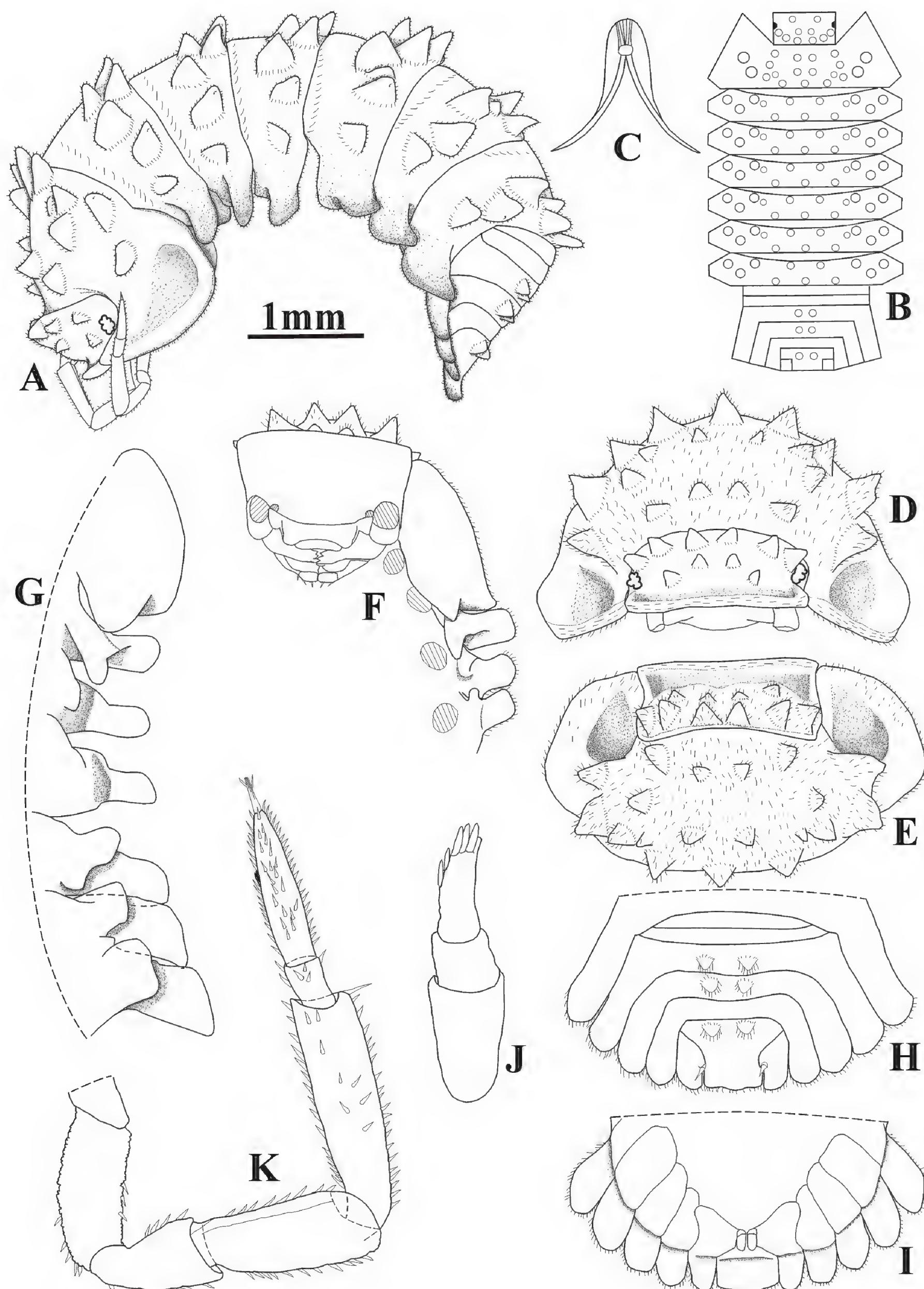


Figure 9. *Diploexochus troglobius* López-Orozco, Borja-Arrieta & Campos-Filho, sp. nov. (♀ paratype, CBUDC-CRU 396) **A** habitus, lateral view **B** dorsal tubercles scheme **C** dorsal scale-seta **D** cephalon and pereonite 1, dorsal view **E** cephalon and pereonite 1, posterior view **F** cephalon and pereonites 1–4, frontal view **G** pereonites 1–7 epimera, ventral view **H** pleotelson and uropods, dorsal view **I** pereonite 7, pleonites 3–5, telson, and uropods, ventral view **J** antennula **K** antenna.

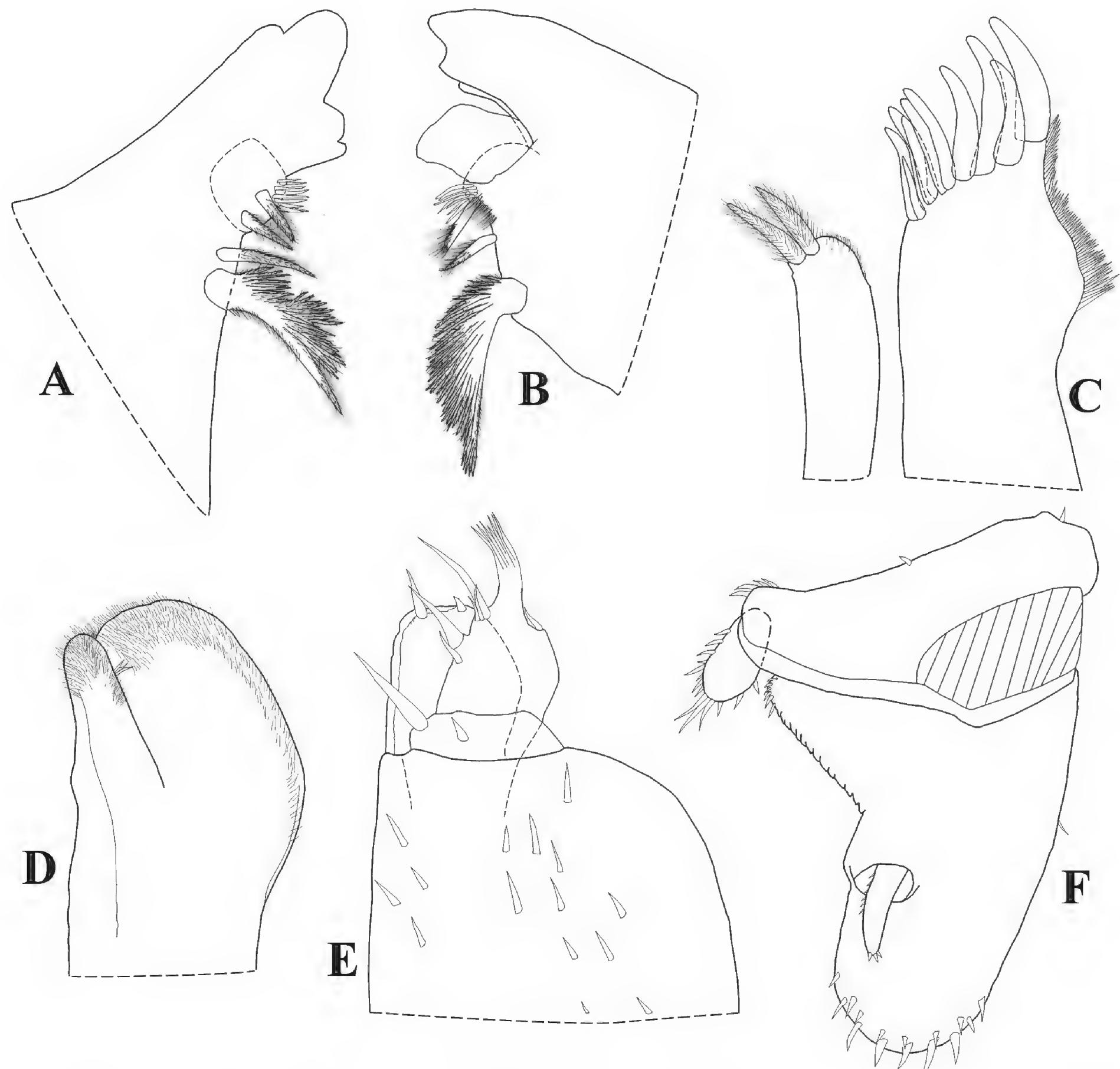


Figure 10. *Diploexochus troglobius* López-Orozco, Borja-Arrieta & Campos-Filho, sp. nov. (♀ paratype, CBUDC-CRU 396) **A** left mandible **B** right mandible **C** maxillula **D** maxilla **E** maxilliped **F** uropod.

Maxilliped basis (Fig. 10E) rectangular, bearing sparse setae; palp with two distinct setae on basal article; endite subrectangular, medial seta surpassing distal margin, distal margin bearing one seta. Pereopods 1–7 merus and carpus with sparse setae on sternal margin; carpus 1 with distal seta cleft at apex; ungual seta and dactylar organ simple not surpassing outer claw. Uropod (Fig. 10F) protopod flattened, enlarged on basal part, distal part elongated and sub-rectangular, distal margin rounded, medial margin concave with L-shaped appearance; exopod as long as endopod inserted dorsally near medial margin below distinct lobe, lobe not extending beyond medial margin; endopod short bearing many short setae. Pleopods 1–5 exopods with mono-spiracular respiratory structures.

Male. Pereopods 1–7 (Fig. 11A, B) without particular modifications. Genital papilla as in Fig. 11C. Pleopod 1 (Fig. 11D) exopod hour-glass shaped, twice as

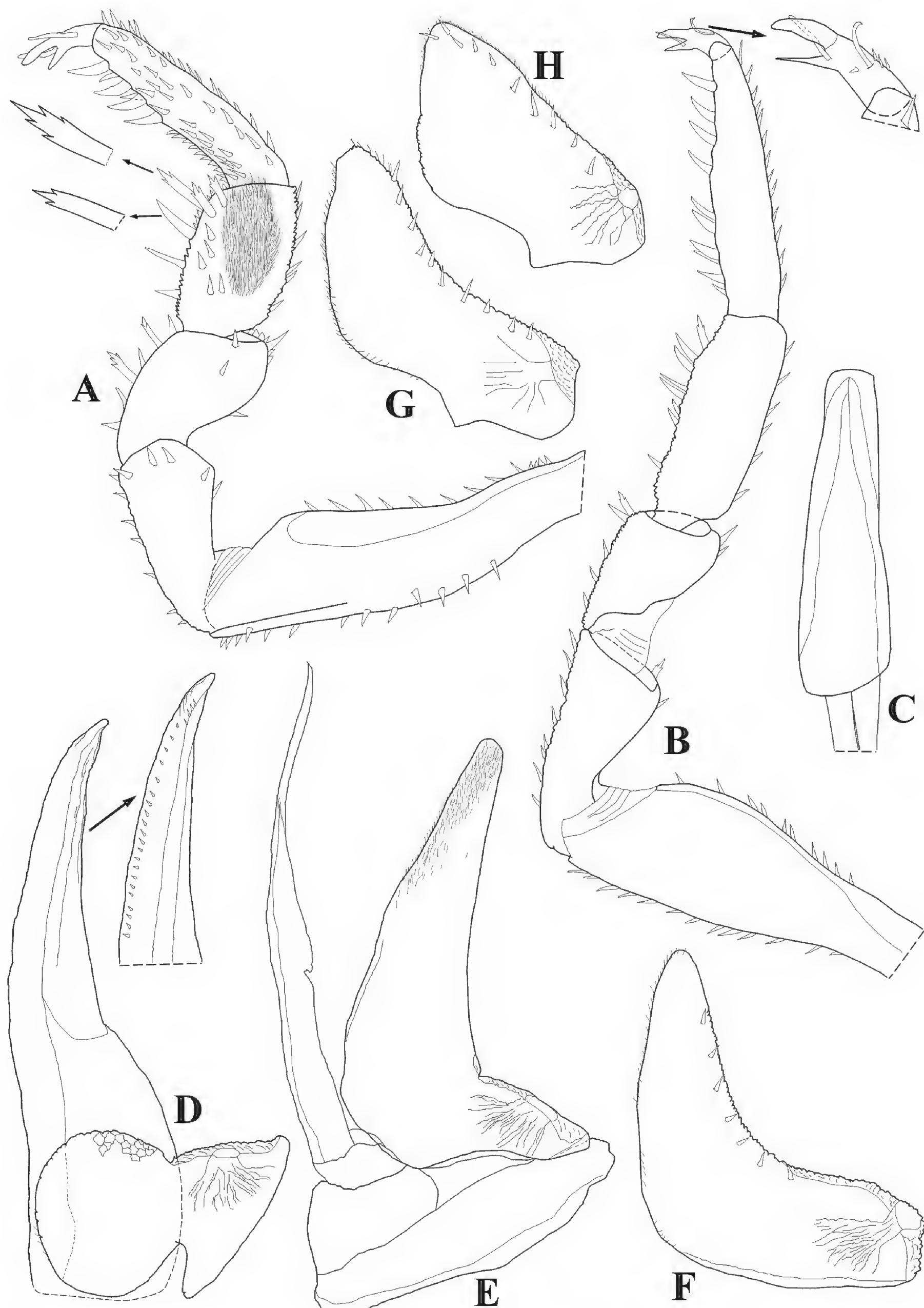


Figure 11. *Diploexochus troglobius* López-Orozco, Borja-Arrieta & Campos-Filho, sp. nov. (♂ paratype, CBUDC-CRU 396) **A** pereopod 1 **B** pereopod 7 **C** genital papilla **D** pleopod 1 **E** pleopod 2 **F** pleopod 3 exopod **G** pleopod 4 exopod **H** pleopod 5 exopod.

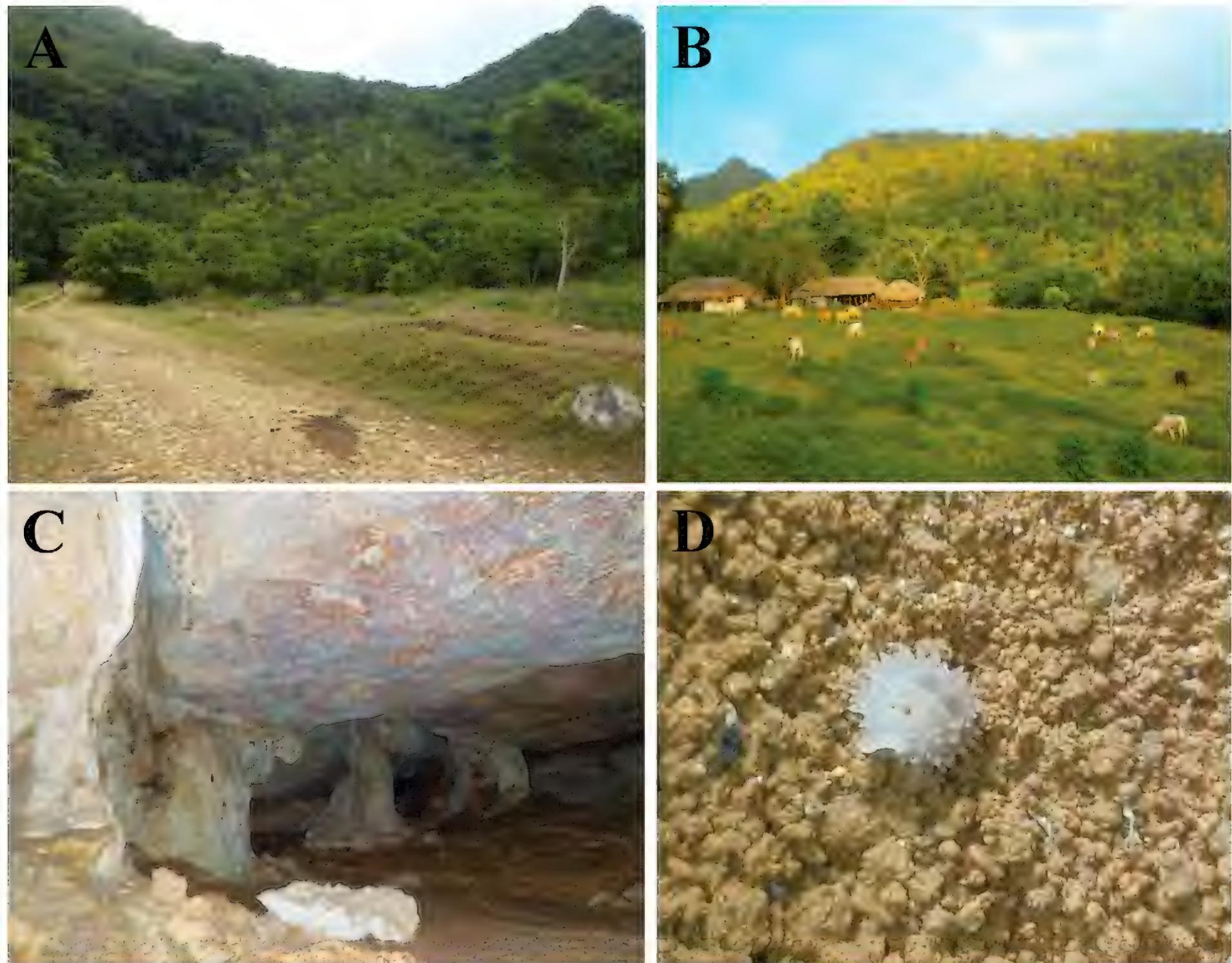


Figure 12. **A** Tropical Dry Forest around Roca Madre Adventure Park, Sucre **B** livestock around Roca Madre Adventure Park **C** Roca Madre Cave Gallery **D** *Diploexochus troglobius* López-Orozco, Borja-Arrieta & Campos-Filho, sp. nov. under limestone rocks.

wide as long, inner portion rounded, outer portion triangular, distal and proximal margins narrow on middle; endopod about three times as long as exopod. Pleopod 2 (Fig. 11E) exopod triangular, outer margin strongly concave; endopod slightly longer than exopod. Pleopod 3–5 exopods as in Fig. 11F–H.

Etymology. Latin: *troglo* + *bio* = cave-dwelling. The new name of the species is an adjective that refers to the troglobitic category of the species.

Remarks. *Diploexochus troglobius* sp. nov. is easily distinguishable from the congeners in the arrangement of the dorsal tubercles of the pleon, dorsal surface with pilose aspect, eyes of four ommatidia, and the shape of the male pleopod 1 exopod.

Natural history. Specimens of *D. troglobius* sp. nov. were collected in the aphotic zone of the Roca Madre Cave, beneath limestone rocks (Fig. 12D). This species is considered troglobitic due to the reduction of body pigments and reduction in the number of ommatidia. In addition, several surveys were conducted outside the cave and other subterranean ecosystems to confirm its restricted distribution. This species is considered endemic to the study area.

Distribution. This species is known only from the type locality at Roca Madre Cave, Sucre, inserted on TDF area (Fig. 1).

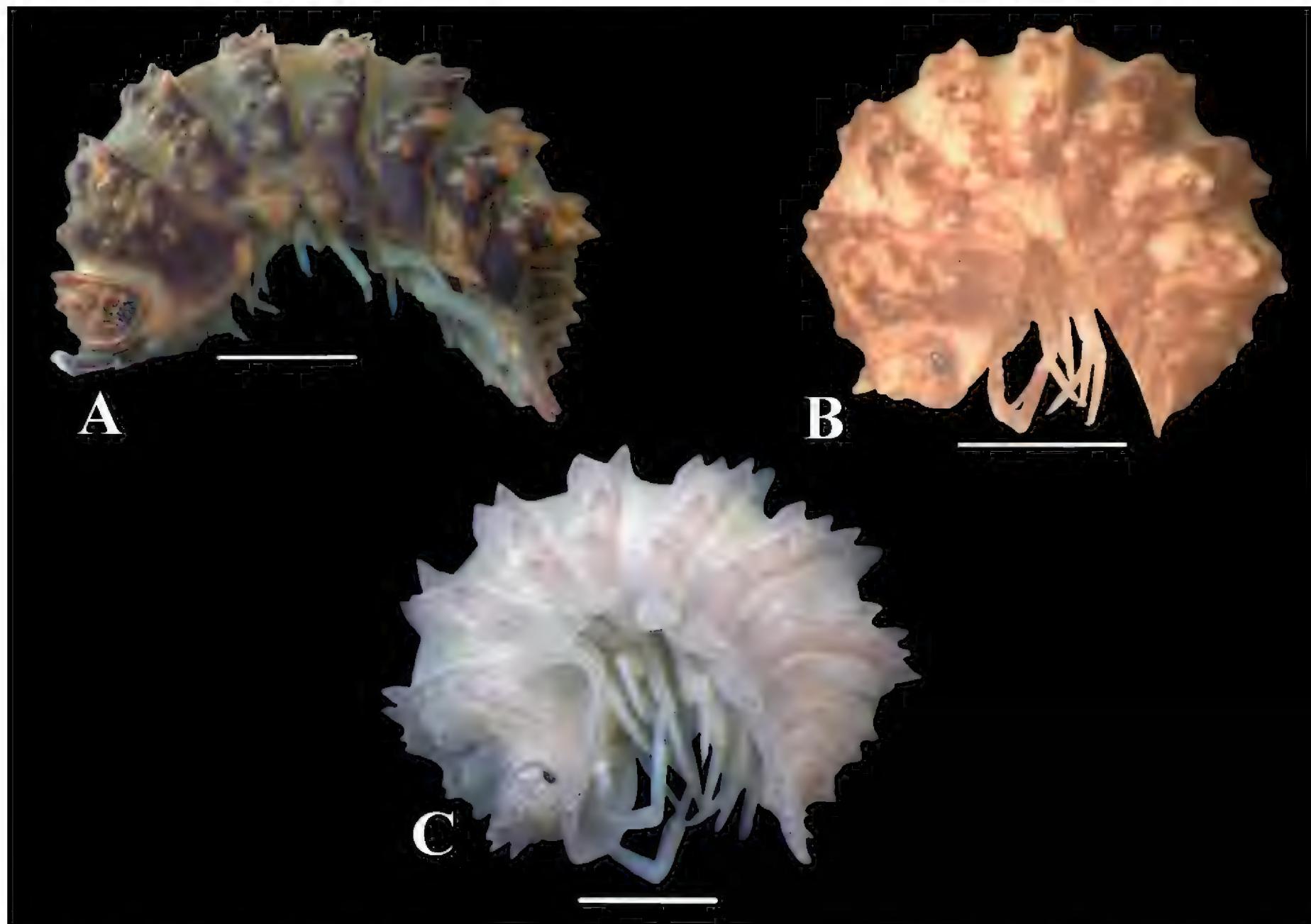


Figure 13. Habitus of the species of the genus *Diploexochus* Brandt, 1833 of Colombia: **A** *Diploexochus brevispinis* (Pearse, 1915), comb. nov. **B** *Diploexochus cacique* López-Orozco, Carpio-Díaz & Campos-Filho, sp. nov. **C** *Diploexochus troglobius* López-Orozco, Borja-Arrieta & Campos-Filho, sp. nov. Scale bars: 1 mm.

Key to species of *Diploexochus*

- 1 Dorsal surface of the pleon with 10 tubercles..... 2
- Dorsal surface of the pleon with < 10 tubercles..... 3
- 2 Pereonite 1 with 24 large, triangular, and acute tubercles.....
..... *D. echinatus* Brandt, 1833
- Pereonite 1 with 21 acute and rectangular tubercles ..
..... *D. obscurus* Cardoso, Bastos-Pereira & Ferreira, 2022
- 3 Cephalon with 8 dorsal tubercles..... 4
- Cephalon with 10 or more tubercles 5
- 4 Pereonites 5–7 with 12 tubercles distributed in two rows; pleonites 3 and 4 with 2 paramedian tubercles ..
..... *D. carrapicho* Campos-Filho, López-Orozco & Taiti, 2023
- Pereonites 5–7 with 7 tubercles distributed in a single row; pleonites 3 and 4 without paramedian tubercles ..
..... *D. exu* Campos-Filho, Sfenthourakis & Bichuette, 2023
- 5 Eyes with 20 or more ommatidia..... 6
- Eyes with 16 or fewer ommatidia 7
- 6 Antennula with nine apical aesthetascs; pereonites 2–6 with 13 tubercles distributed in 2 rows ... *D. spinatus* Cardoso, Bastos-Pereira & Ferreira, 2022
- Antennula with 4 subapically inserted aesthetascs; pereonites 2–6 with 16 tubercles distributed in 2 rows *D. cacique* sp. nov.

- 7 Pleonites 3–4 with a single tubercle on median portion; pereonite 7 with 15 tubercles in 2 rows.....*D. brevispinis* comb. nov.
- Pleonites 3–4 with 2 paramedian tubercles; pereonite 7 with 11 tubercles in 2 rows.....*D. troglobius* sp. nov.

Discussion

The genus *Diploexochus* is distributed in the Neotropical region and is distinguished by the shape and direction of the epimera and pleonites, the frontal shield of the cephalon, and the arrangement of dorsal tubercles (Campos-Filho et al. 2017a, 2023a; Cardoso et al. 2023). In the illustrations of *D. obscurus* provided by Cardoso et al. (2023), pleonite 4 appears to have four tubercles. However, the description mentions that it has two paramedian tubercles, a pattern shared with the species *D. echinatus*. Therefore, a reanalysis of this species is necessary for its correct description and comparison.

The Colombian species of *Diploexochus* are distributed in TDF areas (Fig. 1), considered to host a high level of diversity and endemism, where the species are adapted to extreme environmental conditions, such as drought and extreme temperatures (Alcázar et al. 2021). However, TDF is currently one of the most threatened and least protected tropical biomes on the planet (Murphy and Lugo 1986; Janzen 1988). In Colombia, it is estimated that ~ 720,000 hectares of the original 8 million hectares of TDF remain, and only 5% are under the protection of the National System of Protected Areas (García et al. 2014; Pizano and García 2014). This reduction in vegetation cover is mainly due to various anthropogenic pressures, leading to a loss of biodiversity (Hoekstra et al. 2005; Portillo-Quintero and Sánchez-Azofeifa 2010). Therefore, studies regarding dynamics of populations, including oniscidean species, are necessary to better understand the ecological relations between species and area. Moreover, as in other parts of the world, these organisms could act model to improve conservation and sustainable programs (Solomou et al. 2019; Reboleira et al. 2022).

Subterranean systems are considered biodiversity refuges (Muñoz-Saba et al. 1998a; Culver and Sket 2000; Pipan et al. 2020). The species diversity contained in these habitats mainly depends on strict climatic conditions and energy flow (Ardila 2006; Castellanos-Morales 2018). However, this emerging biodiversity is primarily threatened by the alteration of surrounding natural habitats, anthropogenic pressure, uncontrolled tourism, and mining, among other factors (Restrepo 2007, 2011; Manco et al. 2017; Angarita 2018; Zafra 2021). In Colombia, more than 500 subterranean systems located in 12 biospeleological provinces are known (Muñoz-Saba et al. 1998a, 1998b; Valdivieso 2022). Despite this number, biodiversity research is scarce and isolated for some areas or departments of the country (Muñoz-Saba et al. 1998b, 2013; Vides-Navarro et al. 2015; Angarita 2018; Barriga et al. 2019). Furthermore, most of the country's caves are distributed along transformed agro-ecosystems without any protection (Muñoz-Saba et al. 1998a, 2013). Recently, the National Government enacted the Law number 2237 of 2022, assuring the protection of the Colombian speleological heritage, where environmental authorities will declare protected areas that include speleological biodiversity. However, efforts to conserve these fragile ecosystems are not sufficient, since the number of subterranean ecosystems is still under estimation and the biotic composition, which are sen-

sitive to anthropogenic disturbances, is mostly unknown. It is worth mentioning that this component probably hosts a high degree of endemic species and specific microhabitats or substrates as observed in other studies (Campos-Filho et al. 2017a, 2017b, 2018; López-Orozco et al. 2024a, 2024b). Thus, more studies are needed to assess the conservation status of these ecosystem and quantify and identify its diversity for better conservation efforts.

Regarding the knowledge of oniscideans in Colombian caves, only the species *Ctenorillo papagayoensis* Carpio-Díaz, Borja Arrieta & Campos-Filho, 2023, has been described from the Cueva de Los Papagayos in the department of Santander; *Ctenorillo binomio* Carpio-Díaz, Bichuette & Campos-Filho, 2023, for the Cueva de San Miguel in the department of Bolívar; *Pulmoniscus turbanaensis* López-Orozco, Carpio-Díaz & Campos-Filho, 2017; and *Porcellionides pruinosus* (Brandt, 1833) for the Cueva La Mojana in the department of Atlántico (Carpio-Díaz et al. 2023a, 2023b). Additionally, the genera *Colomboniscus* Vandel, 1972, *Colomboscia* Vandel, 1972, *Sphaeroniscus* Gerstäcker, 1854, *Neosanfilippia* Brian, 1957 (Scleropactidae Verhoeff, 1938), and *Ischioscia* Verhoeff, 1928 (Philosciidae Kinahan, 1857) have been reported from the Cueva de los Papagayos in Santander. The data from the study also include Cueva de Los Indios and Hoyo del Aire in the department of Santander (Sket 1988; Castellanos-Morales et al. 2015; Barriga et al. 2019), although these records do not include species formal descriptions. Regarding other taxa, five studies related to arachnids and a biological inventory of some orders in the Caribbean region have been published (Armas et al. 2015; Cala-Riquelme et al. 2015; Torres-Contreras et al. 2015; Vides-Navarro et al. 2015; García et al. 2022; Moreno-González et al. 2023). This work represents the first record of a troglobitic terrestrial isopod for both the genus and the country, increasing the number of species in the national inventory.

The species *Diploexochus troglobius* sp. nov. is recorded only from Roca Madre cave and has a low population density, supporting both the cave and the species suitable for conservation. Similarly, species such as *Charinus rocamadre* Torres-Contreras, Álvarez García & De Armas, 2015 and *Heterophrynnus caribensis* De Armas, Torres-Contreras & Álvarez García, 2015 (Amblypygi, Charinidae) are under ecological stress due to cattle (Fig. 12B), deforestation, mining, and uncontrolled ecotourism (vandalism). This demonstrates the need to formulate and implement conservation strategies by governmental entities including the scientific community and the general public in decision-making processes.

In the last years, the study of the oniscofauna from Colombia has increased, of which more than 30 epigean species have been described, consolidating a total of 73 species distributed throughout the territory (e.g. López-Orozco et al. 2014, 2016, 2017, 2022; Carpio-Díaz et al. 2016, 2018, 2021, 2023a, 2023b; Campos-Filho et al. 2020; Bravo-Rodríguez et al. 2024). However, the biodiversity of the cave-dwelling isopod species is a new topic and considering the number of caves, this diversity is far from complete.

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Additional information

Conflict of interest

The authors have declared that no competing interests exist.

Ethical statement

No ethical statement was reported.

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Author contributions

Conceptualization: RLBA. Data curation: RLBA, GRNS, MGE. Formal analysis: CMLO, RLBA, ISC-F, YMCD, MEB. Funding acquisition: RLBA, GRNS. Investigation: ISC-F, RLBA, CMLO. Methodology: MGE, RLBA. Software: YMCD. Supervision: MEB, ISC-F. Visualization: RLBA. Writing – original draft: YMCD, ISC-F, MGE, CMLO, MEB, RLBA, GRNS. Writing – review and editing: YMCD, CMLO, MGE, MEB, GRNS, ISC-F, RLBA.

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Data availability

All of the data that support the findings of this study are available in the main text.

References

- Alcázar C, Avella EA, Norden N, García DH, García H, Castellanos C, González-M R (2021) Programa Nacional para la Conservación y Restauración del Bosque Seco Tropical en Colombia-PNCBST, Plan de Acción 2020–2030, Bogotá, Colombia, Ministerio de Ambiente y Desarrollo, 78 pp.
- Anderson LE (1954) Hoyer's solution as a rapid permanent mounting medium for bryophytes. *The Bryologist* 57(3): e242. [https://doi.org/10.1639/0007-2745\(1954\)57\[242:HSAARP\]2.0.CO;2](https://doi.org/10.1639/0007-2745(1954)57[242:HSAARP]2.0.CO;2)
- Angarita T (2018) Breve historia de la bioespeleología en Colombia: perspectivas y oportunidades. I Congreso Colombiano de Espeleología y VIII Congreso Espeleológico de América Latina y el Caribe, 40–58.
- Arcangeli A (1957) I generi *Diploexochus*, *Venezillo*, *Paramardillo* [sic] (crostacei isopodi terrestri). *Bollettino dell'Istituto e Museo di Zoologia dell'Università di Torino* 5: 101–142.
- Ardila CA (2006) *Trichomycterus sandovali*, (Siluriformes, Trichomycteridae) una nueva especie de pez cavernícola para el departamento de Santander, Colombia. *Peces del departamento de Santander* 2: 1–16.
- Armas LF De, Torres-Contreras R, Álvarez DM (2015) Nueva especie de *Heterophrynus* (Amblypygi: Phrynidae) del Caribe Colombiano. *Revista Ibérica de Aracnología* 26: 69–73.
- Barriga JC, Martínez-Torres D, López-Orozco CM, Villarreal O, Murcia MA (2019) Artrópodos terrestres de las cuevas y cavernas de El Peñón (Andes), Santander, Colombia. In: Lasso CA, Barriga JC, Fernández-Auderset J (Eds) *Biodiversidad subterránea y epigea de los sistemas cársticos de El Peñón (Andes)*, Santander, Colombia. Serie Fauna Silvestre Neotropical VII. Instituto de Investigación de Recursos Biológicos Alexander von Humboldt, Bogotá, D. C., Colombia, 99–155. <https://doi.org/10.21068/c2020SFSNVI01>
- Bravo-Rodríguez AE, López-Orozco CM, Nisperuza-Pérez CA, Quirós-Rodríguez JA, Campos-Campos NH (2024) Ampliación del ámbito geográfico de isópodos terrestres (Oniscidea) para el Caribe colombiano y primer registro de *Nagurus nanus* (Trachelipodidae) para Colombia. *Revista de la Academia Colombiana de Ciencias Exactas, Físicas y Naturales* 48(188): 606–622. <https://doi.org/10.18257/raccefyn.2630>
- Cala-Riquelme F, Gutiérrez-Estrada MA, Flórez E (2015) The genus *Loxosceles* Heineken & Lowe 1832 (Araneae: Sicariidae) in Colombia, with description of new cave-dwelling species. *Zootaxa* 4012(2): 396–400. <https://doi.org/10.11646/zootaxa.4012.2.12>
- Campos-Filho IS, Taiti S (2021) Oniscidea taxonomy: present and future. Abstract book of the 11th International Symposium on Terrestrial Isopod Biology. Spinicornis, Ghent, 9.
- Campos-Filho IS, Montesanto G, Araujo PB, Taiti S (2017a) New species and new records of terrestrial isopods (Crustacea, Isopoda, Oniscidea) from Brazil. *Iheringia. Série Zoologia* 107: e2017034. <https://doi.org/10.1590/1678-4766e2017034>
- Campos-Filho IS, Bichuette ME, Montesanto G, Araujo PB, Taiti S (2017b) The first troglobiotic species of the family Pudeoniscidae (Crustacea, Isopoda, Oniscidea) with descriptions of a new genus and two new species. *Subterranean Biology* 23: 69–84. <https://doi.org/10.3897/subbiol.23.20963>
- Campos-Filho IS, Cardoso GM, Aguiar JO (2018) Catalogue of terrestrial isopods (Crustacea, Isopoda, Oniscidea) from Brazil: an update with some considerations. *Nauplius* 26: 2018038. <https://doi.org/10.1590/2358-2936e2018038>

- Campos-Filho IS, López-Orozco CM, Carpio-Díaz YM, Águilar JO, Navas-S GR (2020) Three new species of *Ischioscia* Verhoeff, 1928 (Isopoda, Oniscidea, Philosciidae) from Serranía de Perijá, Andean Cordillera, Colombia Caribbean. *Zoosistema* 42(8): 115–130. <https://doi.org/10.5252/zoosistema2020v42a8>
- Campos-Filho IS, Sfenthourakis S, Gallo JS, Gallão JE, Torres DF, Chagas-Jr A, Horta J, Carpio-Díaz YM, López-Orozco CM, Borja-Arrieta R, Araujo PB, Taiti S, Bichuette ME (2023a) Shedding light into Brazilian subterranean isopods (Isopoda, Oniscidea): expanding distribution data and describing new taxa. *Zoosistema* 45(19): 531–599. <https://doi.org/10.5252/zoosistema2023v45a19>
- Campos-Filho IS, López-Orozco CM, Carpio-Díaz YM, Borja-Arrieta R, Gallão JE, Taiti S, Sfenthourakis S, Bichuette ME (2023b) Everything is similar, everything is different! *Trichorhina* Budde-Lund, 1908 (Oniscidea, Platyarthridae) from Brazilian caves, with descriptions of 11 new species. *Biota Neotropica* 23(4): e20231545. <https://doi.org/10.1590/1676-0611-bn-2023-1545>
- Cardoso GM, Bastos-Pereira R, Ferreira RL (2023) Cave-dwellers *Diploexochus* (Oniscidea, Armadillidae): new species and new records of the genus for Brazil. *Nauplius* 31: e2023008. <https://doi.org/10.1590/2358-2936e2023008>
- Carpio-Díaz YM, López-Orozco CM, Herrera-Medina Y, Navas-S GR, Bermúdez A (2016) Primer registro de *Tylos niveus* y nuevo reporte de *Porcellionides pruinosus* (Oniscidea: Tylidae y Porcellionidae) para Colombia. *Revista de la Academia Colombiana de Ciencias Exactas Físicas y Naturales* 40(156): 4233–4437. <https://doi.org/10.18257/raccefyn.343>
- Carpio-Díaz YM, López-Orozco CM, Campos-Filho IS, Navas GR (2018) Terrestrial isopods (Isopoda: Oniscidea) of the Botanical Garden of Cartagena "Guillermo Piñeres", Colombia, with the description of three new species. *Arthropoda Selecta* 27(4): 301–318. <https://doi.org/10.15298/arthsel.27.4.05>
- Carpio-Díaz YM, López-Orozco CM, Borja-Arrieta R, Campos-Filho IS (2021) A new species and first record of *Trichorhina* Budde-Lund, 1908 (Isopoda, Oniscidea, Platyarthridae) from the Department of Norte de Santander, Colombia. *Nauplius* (29): e2021028. <https://doi.org/10.1590/2358-2936e2021028>
- Carpio-Díaz YM, López-Orozco CM, Borja-Arrieta R, Gutierrez-Estrada M, Campos-Filho IS, Sfenthourakis S, Taiti S, Neita JC, Bermúdez A, Navas-S GR, Bichuette ME (2023a) The genus *Ctenorillo* Verhoeff, 1942 (Oniscidea, Armadillidae) from Colombia: new records, new species, and conservation comments. *Tropical Zoology* 36(3–4): 53–84. <https://doi.org/10.4081/tz.2023.141>
- Carpio-Díaz YM, López-Orozco CM, Borja-Arrieta R, Navas-S GR, Bermúdez A, Neita-Moreno JC, Campos-Filho IS (2023b) New records of terrestrial isopods (Crustacea: Isopoda: Oniscidea) from Colombia. *Arthropoda Selecta* 32(4): 399–408. <https://doi.org/10.15298/arthsel.32.4.04>
- Castellanos-Morales CA (2018) A new species of cave catfish, genus *Trichomycterus* (Siluriformes: Trichomycteridae), from the Magdalena River system, Cordillera Oriental, Colombia. *Biota Colombiana* 19(Sup. 1): 117–130. <https://doi.org/10.21068/c2018.v19s1a10>
- Castellanos-Morales CA, Moreno F, Malagón LM, Arango ÁJ, Pardo DD, Méndez MA (2015) Aportes al conocimiento y uso de los Ecosistemas Subterráneos del Municipio de la Paz (Santander). *Boletín Científico Centro de Museos, Museo de Historia Natural* 19(2): 173–185. <https://doi.org/10.17151/bccm.2015.19.2.10>
- Culver DC, Sket B (2000) Hotspots of Subterranean Biodiversity in Caves and Wells. *Journal of Cave and Karst Studies* 62(1): 11–17.

- Dimitriou AC, Taiti S, Sfenthourakis S (2019) Genetic evidence against monophyly of Oniscidea implies a need to revise scenarios for the origin of terrestrial isopods. *Scientific Reports* 9: 18508. <https://doi.org/10.1038/s41598-019-55071-4>
- Galán C, Herrera FF (1998) Fauna cavernícola: Ambiente, especiación y evolución. *Boletín de la Sociedad Venezolana de Espeleología* 32: 13–43.
- García H, Corzo G, Isaacs P, Etter A (2014) Distribución y estado actual de los remanentes del Bioma de Bosque Seco Tropical en Colombia: insumos para su gestión. In: Pizano C, García H (Eds) *El Bosque Seco Tropical en Colombia*. Instituto de Investigación de Recursos Biológicos Alexander von Humboldt, Bogotá, D. C., Colombia, 229–251 pp.
- García AF, González A, Gutiérrez M (2022) New records and a new cave-dwelling species of Agoristenidae (Arachnida, Opiliones) from Colombia. *Zoosystematics and Evolution* 98(1): 55–63. <https://doi.org/10.3897/zse.98.78202>
- Hoekstra JM, Boucher TM, Ricketts TH, Roberts C (2005) Confronting a biome crisis: global disparities of habitat loss and protection. *Ecology Letters* 8: 23–29. <https://doi.org/10.1111/j.1461-0248.2004.00686.x>
- Hornung E (2011) Evolutionary adaptation of oniscidean isopods to terrestrial life: Structure, physiology and behavior. *Terrestrial Arthropod Reviews* 4: 95–130. <https://doi.org/10.1163/187498311X576262>
- Janzen DH (1988) Tropical dry forest: the most endangered major tropical ecosystem. In: Wilson EO (Ed.) *Biodiversity*. Washington D.C.: National Academy Press, 130–137 pp.
- Leistikow A, Wägele JW (1999) Checklist of the terrestrial isopods of the new world (Crustacea, Isopoda, Oniscidea). *Revista brasileira de Zoologia* 16(1): 1–72. <https://doi.org/10.1590/S0101-81751999000100001>
- López-Orozco CM, Bermúdez A, Navas GR (2014) Primer registro de *Ligia baudiniana* (Crustacea: Isopoda: Oniscidea) para el Caribe colombiano. *Boletín de Investigaciones Marinas y Costeras* 43(1): 195–200. <https://doi.org/10.25268/bimc.invermar.2014.43.1.41>
- López-Orozco CM, Carpio-Díaz YM, Navas GR, Campos-Filho IS (2016) A new species and first record of *Androdeloscia* (Oniscidea: Philosciidae) from Colombia. *Studies on Neotropical Fauna and Environment* 52(1): 18–24. <https://doi.org/10.1080/01650521.2016.1254861>
- López-Orozco CM, Carpio-Díaz YM, Navas GR, Campos-Filho IS (2017) A new species and first record of *Pulmoniscus* Leistikow, 2001 (Isopoda, Oniscidea, Philosciidae) from Colombia. *Nauplius* 25: e2017014. <https://doi.org/10.1590/2358-2936e2017014>
- López-Orozco CM, Carpio-Díaz YM, Borja-Arrieta R, Navas-S GR, Campos-Filho IS, Taiti S, Mateos M, Olazaran A, Caballero IC, Jotty K, Gómez-Estrada H, Hurtado LA (2022) A glimpse into a remarkable unknown diversity of oniscideans along the Caribbean coasts revealed on a tiny island. *European Journal of Taxonomy* 793: 1–50. <https://doi.org/10.5852/ejt.2022.793.1643>
- López-Orozco CM, Campos-Filho IS, Gallo JS, Gallão JE, Carpio-Díaz YM, Borja-Arrieta R, Bichuette ME (2024a) Iron-isopods: new records and new species of terrestrial isopods (Isopoda, Oniscidea) from Brazilian Amazon iron ore caves. *European Journal of Taxonomy* 921: 116–135. <https://doi.org/10.5852/ejt.2024.921.2421>
- López-Orozco CM, Campos-Filho IS, Cordeiro LM, Gallão JE, Carpio-Díaz YM, Borja-Arrieta R, Bichuette ME (2024b) First amphibius Crinocheta (Isopoda, Oniscidea) from Neotropics with a troglobitic status: a relictual distribution. *Zookeys* 1192: 9–27. <https://doi.org/10.3897/zookeys.1192.114230>

- Manco DC, Robles CA, Rojas EE (2017) Descripción de los impactos ambientales causados por el inadecuado manejo en la caverna Sabana de León y cueva Coco Loco, municipio de Manaure, serranía de Perijá, departamento del Cesar – Colombia. *Ingeniare* (23): 25–34. <https://doi.org/10.18041/1909-2458/ingeniare.2.2880>
- Montesanto G (2015) A fast GNU method to draw accurate scientific illustrations for taxonomy. *ZooKeys* 515: 191–206. <https://doi.org/10.3897/zookeys.515.9459>
- Montesanto G (2016) Drawing setae: A GNU way for digital scientific illustrations. *Nauplius* 24(0): e2016017. <https://doi.org/10.1590/2358-2936e2016017>
- Moreno-González JA, Gutierrez-Estrada M, Prendini L (2023) Systematic revision of the whip spider family Paracharontidae (Arachnida: Amblypygi) with description of a new troglobitic genus and species from Colombia. *American Museum Novitates* (4000): 1–36. <https://doi.org/10.1206/4000.1>
- Muñoz-Saba Y, Andrade-Pérez GI, Baptiste-Ballera BLG, Salas D, Villarreal H, Armenteras D (1998a) Conservación de los Ecosistemas Subterráneos en Colombia. Biosíntesis, 10: 1–4.
- Muñoz-Saba Y, Andrade GI, Baptiste LG (1998b) Cuevas y Cavernas. Tomo I. In: Chávez ME, Arango N (Eds) Informe Nacional sobre el Estado de la Biodiversidad (1997) Colombia. Instituto de Investigación de Recursos Biológicos Alexander von Humboldt, PNUMA, Ministerio del Medio Ambiente, Bogotá, D. C., Colombia, 164–175 pp.
- Muñoz-Saba Y, González-Sánchez I, Calvo-Roa N (2013) Cavernas de Santander, Colombia: Guía de campo. Serie de Guías de campo del Instituto de Ciencias Naturales, Bogotá, Instituto de Ciencias Naturales, Universidad Nacional de Colombia, 325 pp.
- Murphy PG, Lugo AE (1986) Ecology of tropical dry forest. *Annual Review of Ecology and Systematics* 17: 67–68. <https://doi.org/10.1146/annurev.es.17.110186.000435>
- Paoli P, Ferrara F, Taiti S. 2002. Morphology and evolution of the respiratory apparatus in the family Eubelidae (Crustacea, Isopoda, Oniscidea). *Journal of Morphology* 253(3): 272–289. <https://doi.org/10.1002/jmor.10008>
- Pearse A (1915) An account of the Crustacea collected by the Walker Expedition to Santa Marta, Colombia. *Proceedings of the United States National Museum* 49: 531–556. <https://doi.org/10.5479/si.00963801.49-2123.531>
- Pipan T, Deharveng L, Culver DC (2020) Hotspots of subterranean biodiversity. *Diversity* 12(5): 209. <https://doi.org/10.3390/d12050209>
- Pizano C, García H (2014) El Bosque Seco Tropical en Colombia, Instituto de Investigación de Recursos Biológicos Alexander von Humboldt (IAvH). Bogotá, DC, Colombia, 353 pp.
- Portillo-Quintero CA, Sánchez-Azofeifa GA (2010) Extent and Conservation of tropical dry forests in the Americas. *Biological Conservation* 143: 144–155. <https://doi.org/10.1016/j.biocon.2009.09.020>
- Reboleira ASP, Eusébio RP, Taiti S (2022) Species conservation profiles of cave-adapted terrestrial isopods from Portugal. *Biodiversity data journal* 10: e78796. <https://doi.org/10.3897/BDJ.10.e78796>
- Restrepo C (2007) El deterioro del sistema kárstico de la Danta (Sonsón-Antioquia). In: Património Geológico, Arqueológico e Mineiro em Regios Cársicas. Batalha, 47–53.
- Restrepo C (2011) El sistema kárstico de la Danta (Sonsón - Antioquia) Colombia. *Dyna* 78(169): 239–246.
- Richardson H (1912) Terrestrial isopods of Colombia. *Mémoires de la Société des Sciences Naturelles de Neuchâtel* 5: 29–32.
- Rodríguez-Cabrera TM, Armas LF De (2023) Taxonomy of the enigmatic genus *Acanthoniscus* Gosse, 1851 (Isopoda: Oniscidea: Armadillidae), from Jamaica, with the

- description of a new species. *Nauplius* 31: e2023006. <https://doi.org/10.1590/2358-2936e2023006>
- Schmalfuss H (2003) World catalog of terrestrial isopods (Isopoda: Oniscidea). Stuttg Beitr Naturkd 654: 1–341.
- Schmidt C, Leistikow A (2004) Catalogue of genera of the terrestrial Isopoda (Crustacea: Isopoda: Oniscidea). *Steenstrupia* 28 (1): 1–118.
- Sfenthourakis S, Taiti S (2015) Patterns of taxonomic diversity among terrestrial isopods. *ZooKeys* 515: 13–25. <https://doi.org/10.3897/zookeys.515.9332>
- Sket B (1988) Speleobiological investigation in the Colombian Andes 1984. Biolosky. *Vestnik* 36(2): 52–62.
- Solomou AD, Sfougaris AI, Sfenthourakis S (2019) Terrestrial isopods as bioindicators for environmental monitoring in olive groves and natural ecosystems. *Journal of Natural History* 53(27–28): 1721–1735. <https://doi.org/10.1080/00222933.2019.1658821>
- Taiti S (2017) Biologia e biogeografia degli isopodi terrestri (Crustacea, Isopoda, Oniscidea). Atti Accademia Nazionale Italiana di Entomologia, Anno 65: 83–90.
- Taiti S, Paoli P, Ferrara F (1998) Morphology, biogeography, and ecology of the family Armadillidae (Crustacea, Oniscidea). *Israel Journal of Zoology* 44(3–4): 291–301.
- Torres-Contreras R, Álvarez DM, Armas LF De (2015) Una nueva especie de *Charinus* Simon, 1892 (Amblypygi: Charinidae) del Caribe Colombiano. *Revista Ibérica de Aracnología* 27: 145–148.
- Valdivieso GE (2022) Parámetros espeleométricos para levantamientos espeleológicos de cavidades colombianas. *Mundo Subterráneo* 8: 2–22.
- Van Name WG (1936) The American land and freshwater isopod Crustacea. *Bulletin of the American Museum of Natural History* 71: 1–535.
- Vandel A (1952) Étude des isopodes terrestres récoltés au Vénézuela par le Dr. G. Maruzzi. *Memorie del Museo Cívico di Storia Naturale di Verona* 3: 59–203.
- Vides-Navarro F, Montes-Calderón A, Fernández-Cuello G, Rojas-Martínez E (2015) Caracterización espeleológica e inventario biológico de la Caverna del Diablo en el municipio de Becerril, Departamento del Cesar. *Respuestas* 20(2): 93–104. <https://doi.org/10.22463/0122820X.356>
- Zafra D (2021) Propuesta para la conservación de cuevas y cavernas en la Región Andina de Colombia. Tesis de especialización, Universidad Pontificia Bolivariana, Bucaramanga, Colombia, 89 pp.